Population structure and dispersal of black-backed woodpeckers, a disturbance-dependent species

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EXECUTIVE SUMMARY

Ecological connectivity is especially important for species that rely on habitats that are only temporally available, such as early post-fire habitat. Black-backed woodpeckers are a highly specialized species that occupies early post-fire habitat for approximately three to five years after a fire. As such, they are directly affected by fire and forest management decisions due to their dependence on food and nesting resources provided by standing dead trees. Our primary goal was to describe the population structure and dispersal dynamics of black-backed woodpeckers to better inform fire and forest management activities that affect connectivity.

We used both population and individual-based genetic approaches to assess barriers to movement in black-backed woodpeckers. Furthermore, we tested if male and female woodpeckers exhibited the same movement patterns. Three genetic groups were identified, a large, genetically continuous population that spans from the Rocky Mountains to Quebec, a small isolated population in South Dakota and a separate population in the western portion of their distribution (Oregon). Patterns of genetic diversity suggest high gene flow mediated by both males and females within the continuous boreal forest. However, male-mediated gene flow is the main form of connectivity between all the populations. The smaller populations of South Dakota and Oregon are separated by large areas of unforested habitat, which apparently serves as a behavioral barrier to movement of female woodpeckers.

We documented the effect of frequent colonization of highly ephemeral habitats on the fine-scale genetic structure of a fire-specialist, the black-backed woodpecker, compared to a more generalist species, the hairy woodpecker. Black-backed woodpeckers displayed positive spatial genetic structure at a larger spatial scale (90 km) than hairy woodpeckers (45 km), likely due to dispersing farther distances to search out optimal habitat patches. We found black-backed woodpeckers likely disperse less than 100 km, providing the first details on the spatial scale that these burned areas provide migrants. Our results confirm banding studies that show hairy woodpeckers only disperse ~40 km. Black-backed woodpeckers likely move longer distances because they are more reliant on burned forest for habitat, whereas hairy woodpeckers can successfully reproduce in many habitat types. We tested for differences in spatial structure between sexes in both species and detected a pattern consistent with male-biased dispersal in black-backed woodpeckers and female-biased dispersal in hairy woodpeckers. Finally, we detected a temporal increase in genetic correlation among black-backed woodpeckers within habitat patches, but not for hairy woodpeckers. This pattern provides support for the hypothesis that juvenile black-backed woodpeckers may delay dispersal to exploit habitat patches while they are optimal, but hairy woodpeckers likely disperse from the natal territory. Burned forests have long been thought to be source habitat for highly specialized woodpeckers, such as black-backed woodpeckers. It may be that unburned forests are a more detrimental sink to black-backed populations than hairy woodpecker populations, forcing black-backed woodpeckers to search farther for burned forest.

INTRODUCTION

Wildfire plays a central role in shaping western landscapes, and therefore, many species are adapted to post-fire habitat. In the western United States, recent large-scale, high-severity fires have been attributed to the suppression of fire in forest systems for the past century. As a result, both salvage logging and fuel reduction treatments are becoming increasingly important land management tools. However, a more complete understanding of the effects these actions have on wildlife populations is necessary to take an ecosystem management approach to fire management.

The black-backed woodpecker (*Picoides arcticus*; BBWO) is perhaps the most commonly cited example of a fire-specialist (Dixon and Saab 2000, Brawn et al. 2001, Hutto 2008, Nappi and Drapeau 2009). Black-backed woodpeckers live six to eight years, yet they only occupy fire-disturbed areas for three to five years post-fire (Murphy and Lehnhausen 1998, Dixon and Saab 2000, Saab et al. 2007, Vierling et al. 2008). Peak densities occur two to four years following the burn (Saab et al. 2007, Nappi and Drapeau 2009), which corresponds to high wood-boring beetle (Coeloptera: Buprestidae and Cerambycidae) densities in post-burn habitats (Otvos 1979), which is their primary prey (Murphy and Lehnhausen 1998). After four to five years, this ephemeral and highly dynamic habitat becomes sub-optimal due to a reduction in food resources. While black-backed woodpeckers have been documented in unburned areas such as beetle-killed stands, nest success tends to be extremely high (80 – 100%) in areas that burned at moderate to high severity (Vierling et al. 2008) and much lower in unburned areas (40 – 65%; Bonnot et al. 2008, Nappi and Drapeau 2009) leading to the assumption that these unburned areas are not optimal habitat for black-backed woodpeckers to nest. In fact, Hutto (1995) suggested that burned areas are necessary to maintain black-backed woodpecker populations with moderate to high severity burned areas serving as source habitats and unburned areas acting as sink habitats. Concordantly, Hoyt and Hannon (2002) proposed that the long-term persistence of black-backed woodpecker populations may depend on the frequency of recently burned patches within their dispersal range. More recently, Nappi and Drapeau (2009) used a combination of empirical reproductive success data within burned areas and source-sink models to test if burned areas do in fact serve as source habitats and concluded that burned forests may serve as a source soon after a fire in certain fire severities.

Black-backed woodpeckers are directly affected by fire management decisions due to their dependence on early post-fire habitat (Hutto 1995, Murphy and Lehnhausen 1998, Dixon and Saab 2000). In Montana, BBWO are classified as a Species of Greatest Concern (Tier 1) (Montana Fish, Wildife and Parks 2005). BBWO conservation concerns recognized by the state of Montana include timber harvest, fire suppression and salvage logging (Montana Fish, Wildife and Parks 2005). Additionally, monitoring of BBWO populations is an integral part of determining the current and future status of BBWO in Montana. However, monitoring data cannot be interpreted correctly without information on population structure and movement among populations

Federal and State land management agencies have directives to 1) monitor populations of BBWO and 2) ensure there are reservoir populations to colonize newly burned habitats. The challenge in defining populations of fire-associated species lies in the ephemeral nature of habitat patches. Species reliant on early post-fire habitat, such as woodpeckers, tend to occupy burned patches only a few years and then move on to newly created habitats. This temporal variation in patch availability creates challenges in defining population boundaries necessary to interpret population trends and in managing species' habitat. Monitoring birds within a specific burned area does not constitute a population, yet there is currently no information available on the appropriate scale to monitor a BBWO population (i.e. complex of burns, National Forest, Region). Second, the ability of birds to colonize newly burned habitats is based directly on their dispersal ability.

OBJECTIVES

Our primary goal is to describe the population structure and dispersal dynamics of black-backed woodpeckers to better inform population management. In addition, we will contribute to the field of disturbance ecology by exploring the effects of disturbance on ecological connectivity. This information can be used to design the proper scale of sampling and interpreting of monitoring data. We will then determine average dispersal distance, which can be used to prioritize decisions concerning the anthropomorphic influences on disturbance such as prescribed fire and salvage logging. This information is necessary to understand habitat connectivity and to perform the required population monitoring and management of BBWO, a fire-dependent species. We will accomplish this by answering the following questions:

Research Questions:

1) What is a breeding population?
2) What is the average dispersal distance of black-backed vs. hairy woodpeckers?
3) How does the observed pattern of genetic variation inform the monitoring and management of populations?

STUDY DESIGN AND FIELD METHODS

We designed our study in a hierarchical manner to assess genetic structure at multiple scales. We had two field locations in western Montana with three burned areas within 50 km of each other to assess fine-scale structure within and among burned areas (Figure 1). These areas ranged in size from approximately 4,000 to 16,000 hectares, burned in 2003, and sampling occurred between 2004 – 2007. In addition, we collected samples from both species of woodpeckers as part of a larger scale study in Oregon, South Dakota, and Eastern Canada (Figure 1). Additional black-backed woodpecker samples were collected from Alberta and Idaho. .

Sampling and DNA extraction

Blood or feather samples were collected in seven sampling locations: Alberta, Idaho, Oregon, west-central (W.C.) Montana, northwest (N.W.) Montana, South Dakota, and Quebec (Figure 1). Blood samples were collected from adults caught at the nest site with either a hoop net or mist net during the 2004-2007 breeding seasons. Blood samples were stored at room temperature in a lysis buffer (Longmire et al. 1988). Individuals were color banded to avoid resampling in concurrent years and to record any dispersal events. We did not sample offspring in the nests to reduce sampling related individuals. A portion of the Idaho samples (n = 29) were feathers collected as part of a radio telemetry study conducted in 1998-2000 (Dudley and Saab 2007); Quebec samples were collected in 2000-2001. The latitude and longitude of individual sample locations was recorded. DNA was extracted from both blood and feather tissues using a DNeasy Tissue

Extraction Kit (QIAGEN Inc.). Blood was incubated for 2 – 24 hours with a final elution of 200 ul and feathers were kept on a rocker for 48 hours with a final elution of 100 ul to increase final DNA concentration.

Genotyping and Sequencing

Mitochondrial DNA (mtDNA) was amplified using the polymerase chain reaction (PCR) and primers (L14841 and H15149) for the cytochrome b region (Kocher et al.1989). Samples were genotyped at eleven microsatellite loci: *C111*, *C115*, *D118*, (Vila et al. 2008); *RCW4* (added tail), *RCW5*, *RCW17* (added tail), (Mullins and Haig in review); *DIU1*, *DIU3*, *DIU4*, (Ellegren et al. 1999); *HrU2*, (Ellegren 1992); *Lox4*, (Piertney et al. 1998). We added 'GTTTCTT' to the 5' end of the reverse primer of RCW4 and RCW17 to promote the addition of adenine (Brownstein et al. 1996).

Genetic Variation

Microsatellite markers were tested for departure from Hardy-Weinberg proportions and gametic disequilibrium in GENEPOP (version 1.2; Raymond and Rousset 1995). We calculated observed and expected heterozygosity and average number of alleles/locus in GDA (version 1.1; Lewis and Zaykin 2001). Allelic richness and F_{IS} were calculated in FSTAT. The presence of null alleles, dropout of large alleles and errors due to stuttering were tested using MICRO-CHECKER (Van Oosterhout et al. 2004). For mtDNA, haplotype diversity (h) and nucleotide diversity (π) were calculated using DnaSP (version 4.50; Rozas et al. 2003). Haplotype richness was calculated by taking the mean number of haplotypes observed when sampling 21 (minimum number) haplotypes with replacement from the frequency distribution of haplotypes created by sampling 10,000 times.

Black-backed woodpeckers: What is a breeding population?

Population-based Analyses

We calculated pairwise F_{ST} (Weir and Cockerham 1984) among all sampling locations and tested for isolation by distance based on $F_{ST}/(1- F_{ST})$ vs. linear geographic distance among sample sites using Mantel tests (Mantel 1967) in the ade4 (Dray et al. 2007) package in the R software environment (http://www.r-project.org/).

Because our study was conducted at such a large spatial scale, we began by assessing hierarchical population structure where individuals at a sampling location were considered one group. We conducted an analysis of molecular variance (AMOVA; ARLEQUIN 3.11; Excoffier et al. 2005) and a spatial analysis of molecular variance (SAMOVA; Dupanloup et al. 2002;) for both marker types. We tested five different hierarchical groupings (Table 1) and tested for significance of the variance components using 1000 permutations. Populations were identified by maximizing the among group percent of variation (F_{CT}) as recommended by Dupanloup et al. (2002). We used principal component analysis (PCA) to visualize how sample sites clustered using PCAGEN (http://www2.unil.ch/popgen/softwares/pcagen.htm).

Individual-based Analyses

We used a Bayesian clustering approach,GENELAND (version 3.1.4; Guillot et al. 2005b), to determine the number of clusters based on gametic disequilibrium and deviations from Hardy-Weinburg proportions. We used the spatially explicit approach which can infer spatial discontinuities in genetic data when incorporating the spatial location of individual samples as well as a user-defined uncertainty around sampling locations. Although the algorithm in GENELAND simultaneously estimates all the parameters, Guillot et al. (2005a), recommend a two-step approach. The first step infers the number of populations (*K*) and the second step holds *K* constant to assign individuals to populations.

We began the GENELAND analyses by running 10 replicates with the following parameters: maximum rate of Poisson process of 274 (equal to sample size as recommended by Guillot et al. 2005a), allowed *K* to vary from 1 to 10, maximum number of nuclei of 825 (roughly three times the sample size as recommended by Guillot et al. 2005a), 500,000 MCMC iterations with a burn-in period of 100,000 iterations, the Dirichlet model (which has been shown to perform better than alternate models available in GENELAND; Guillot et al. 2005a) in which allele frequencies are assumed to be independent, spatial coordinates with an uncertainty of 5 km.

To test the robustness of our GENELAND results, we varied several input parameters to see if we obtained the same estimate of *K*. We varied uncertainty on the spatial coordinates from 0 – 50 km. We ran the same analysis as above with the nine loci dataset without using the null allele model to determine if the results would change based on these two different models.

Once *K* was identified, we ran 100 replicates of the model with the same parameters as above and *K* held constant. We ranked the models by mean logarithm of posterior probability and conducted post-processing analyses on the top ten models runs. We used a burn-in period of 100,000 iterations, a spatial domain of 400 pixels along the X axis and 200 pixels along the Y axis and checked the runs visually for consistency.

Sex-biased Movement Patterns

Sex-biased movements can be estimated using genetic techniques by measuring the proportion of recent immigrants that are male versus female in a population. However, it is often difficult to sample extensively enough to capture recent immigrants. Another method is examining different patterns of genetic structure in sex-linked markers compared to autosomal markers. We were interested in movements that occur at irregular time intervals and did not anticipate sampling recent immigrants, so we focused on the comparing patterns of genetic structure from mtDNA, which is maternally inherited, to autosomal microsatellites.

Estimates of F_{ST} based on microsatellite markers can be biased low due to their highly variable nature (Hedrick 2005a). To account for this potential bias, we calculated standardized estimates of pairwise estimates of F_{ST} (G_{ST}') for both marker types (Hedrick 2005a, Meirmans 2006). The maximum F_{ST} was calculated by recoding each population to have unique alleles/haplotypes to maximum among population variation, while maintaining observed levels of variation (Hedrick 2005a, Meirmans 2006). We also plotted observed and standardized F_{ST} values on plots that show the expected values of F_{ST} for both mtDNA and nuclear markers under island model of migration and following isolation (Zink and Barrowclough 2008).

Black-backed and hairy woodpeckers: What is the average dispersal distance of black-backed vs. hairy woodpeckers?

Global spatial autocorrelation analyses

Only samples collected within five years after an area burned are included in these analyses. To examine within patch dispersal patterns, we performed global spatial autocorrelation analyses (Smouse and Peakall 1999, Double et al. 2005) in GenAlEx6 (Peakall and Smouse 2006). Global autocorrelation analysis is a multivariate approach which can detect a spatial pattern generated by multiple loci simultaneously (Smouse and Peakall 1999). This approach calculates a genetic autocorrelation coefficient (*r*) for a specified set of distance classes from a genetic distance matrix and geographic distance matrix. Significant spatial structure is measured using both bootstrapping and permutation tests as described in Peakall et al. (2003). Specifically, we used bootstrapping (1000) to calculate 95% error bars around the estimate of *r* and assumed significance when the error bar did not cross zero, which is considered the conservative approach (Peakall and Smouse 2006). Permutation tests (1000) calculate a 95% confidence envelope and significance is assumed when the estimate of *r* falls outside the confidence envelope. Permutation tests provide a more robust estimate of significance when sample sizes are small because they use the entire data set which provides more information (Peakall and Smouse 2006).

The genetic correlation matrix contains pairwise individual to individual genetic distances via the distance methods of Smouse and Peakall (1999). The geographic distance matrix was calculated from latitude and longitude locations (collected as WGS 84 data in decimal degrees) at the nest site where the bird was captured.

To determine the largest spatial scale that genetic structure among individuals could be detected, we conducted a global spatial autocorrelation that included all samples across the study and used the even sample size per distance class option. Once we broadly determined the scale at which spatial structure among individuals exists for each species, we performed a spatial autocorrelation analysis at a smaller scale to determine more precisely the scale at which there is no longer a signature of autocorrelation. To test for positive spatial autocorrelation expected from limited dispersal, we used a one-tailed test of significance that the estimated $r >$ permuted r with a significance level of 0.05. We tested for differences between dispersal patterns in males and females by performing global spatial autocorrelation on males and females separately.

Local autocorrelation analyses

We used two different approaches to assess if a genetic correlation among individuals was higher within burned areas as compared to among burned areas. We limited these analyses to burned areas in which we were able to collect samples from > 10 individuals over the course of the study. First, we employed a two-dimensional local spatial autocorrelation (2D LSA) that calculates a local autocorrelation (*lr*) for each focal point and a specified subset of *n* neighboring points. We calculated a 2D LSA for the five nearest neighbors and permutation tests were used to calculate significance. While multiple comparisons are involved in this type of analyses, Bonferroni corrections are not necessary because we are only looking at a small, specific subset of points (Peakall and Smouse 2006), therefore we used a P = 0.05 to indicate significant *lr* values. We used *SigmaPlot 11* to create bubble plots to visualize significant *lr* values.

To test if relatedness increased over time, as expected if juveniles were remaining near the natal territory, we calculated the genetic correlation coefficient (*r*) within each burned area and used both random permutations (1000) and bootstrap (1000) methods to calculate 95% confidence limits in order to assess if *r* was greater than expected. We calculated *r* within each area for the first, second and third years. The second and third years include cumulative samples, that is, year two includes samples from both year one and two. We were unable to conduct this temporal analysis for hairy woodpeckers due to smaller sample sizes per year.

RESULTS

Genetic variation

We found 16 variable sites in the 325 base pairs sequenced in the cytochrome b region of the mitochondrial genome. We identified 18 haplotypes, ranging from two in South Dakota to 12 in Quebec (Table 2). Haplotype diversity (h) and nucleotide diversity (π) were highest in Idaho (h = 0.616, π = .0035) and lowest in South Dakota (h = 0.095, π = 0.0006). One haplotype was very common (> 60%), a second was relatively common (16%) and eight haplotypes were only detected once (Table 2).

Ten of the eleven microsatellites were polymorphic in all the populations; Locus DIU1 was monomorphic in South Dakota. After correcting for multiple comparisons (Rice 1989), two loci had departures from H-W proportions, *DIU1* and *RCW17*; four pairwise comparisons were significant for gametic disequilibrium. The average number of alleles per locus ranged from 3.64 in South Dakota to 6.91 in Quebec. Allelic richness was lowest in South Dakota (3.57) and highest in Alberta (6.36). South Dakota had the lowest levels of heterozygosity (H_O = 0.46), other sites ranged from (0.51-0.62) (Table 2).

Null alleles were likely present at three loci: *DIU1*, *RCW17* and *C111*. Both *DIU1* and *RCW17* had relatively high estimated frequencies of null alleles (0.20, 0.15) while the estimated frequency of the null allele at *C111* occurred at a relatively low frequency (0.06). We conducted most analyses on both a full and reduced data set, with the same general pattern resulting from both datasets; most results presented are from the dataset with nine loci, after removing *DIU1* and *RCW17*. GENELAND results are from the full dataset because the algorithm implemented can estimate frequencies of null alleles.

Black-backed and hairy woodpeckers: What is the average dispersal distance of black-backed vs. hairy woodpeckers?

Population-based Analyses

Samples collected from sites within the continuously distributed areas had lower pairwise F_{ST} values for both mtDNA and microsatellite data (Table 3). For mtDNA, pairwise F_{ST} values for the continuous sites ranged from 0.00-0.11 while the fragmented sites ranged from 0.36-0.75. Overall, pairwise F_{ST} values for microsatellite data was much lower, with values among the continuous sites ranging from 0.006 – 0.022 and from 0.035-0.094 among the fragmented sites. The grouping of sites within the continuously distributed locations as one population was supported by AMOVA (Table 1), SAMOVA, and PCA (Figure 2). Due to similar results between the AMOVA and SAMOVA, we only present AMOVA results. PCA reveals that, for both marker types, all sites within the continuously distributed area cluster tightly together and Oregon and South Dakota cluster separately from the continuous sites and each other (Figure 2).

Individual-based Analyses

GENELAND identified three populations (K=3), with all ten runs identifying K= 3 with the highest probability. Individuals assigned to populations with a high probability, with only six individuals ambiguously assigned with probability of assignment =>0.99 (Figure 3). Geographic barriers to gene flow were identified with probability of assignment contours (Figure 3).

Sex-biased movement patterns

Pairwise F_{ST} estimates for microsatellite data between the continuous and fragmented sites were 4 – 5 times lower than you would predict based on island model of migration at mutation-drift equilibrium using the following equation (Brito et al 2007): $F_{ST(msat)} = F_{ST(mtDNA)} /4 - 3*F_{ST(mtDNA)}$ (Figure 4). After standardization, pairwise F_{ST} estimates for microsatellite data between the continuous and fragmented sites were > 2 times lower than expected based on Wright's island model of migration. For example, pairwise $F_{ST(mtDNA)} = 0.49$ between Oregon and the continuous population; under the island model, the expected $F_{ST(msat)} = 0.19$, observed $F_{ST(msat)} = 0.04$. After standardizing, the standardized pairwise $F_{ST(mtDNA)} = 0.72$ between Oregon and the continuous population, the expected $F_{ST(msat)} = 0.39$, observed standardized $F_{ST(msat)} = 0.17$ (Table 4).

Black-backed and hairy woodpeckers: What is the average dispersal distance of black-backed vs. hairy woodpeckers?

Global spatial autocorrelation

In black-backed woodpeckers, we detected significantly positive genetic correlation (*r*) at less than 229 km (Figure 5a) when conducting global spatial autocorrelation using variable distance classes up to the largest spatial scale (3500 km). We then conducted a global spatial autocorrelation analysis with 15 km distance classes and a maximum distance of 225 km. The 15 km distance classes represent the scale of within fire dynamics, that is, all birds within a particular burned area were located within 15 km of each other. When examining smaller distance classes (15km), black-backed woodpeckers displayed significantly positive *r*-values in distance classes up to 90 km (Figure 6a; Table 5). Female black-backed woodpeckers showed a similar pattern to the entire population, with significantly positive *r*-values in distance classes up to 75 km which is consistent with a pattern of restricted dispersal (Figure 6c; Table 5). Male black-backed woodpeckers only consistently had significantly positive *r*-values at the smallest distance class (15km; Figure 6b, Table 5); results from the one-tailed test were significant in the 60 km class as well (Table 5). The positive autocorrelation among males within the 15 km class is likely a result of related males within burned areas.

Hairy woodpeckers consistently displayed significantly positive *r*-values at less than 51 km (Figure 5b). In the smaller-scale analysis with 15 km distance classes, hairy woodpeckers consistently had significantly positive *r*-values up to 45 km (Figure 6d; Table 5). Several of the larger distances classes (e.g. 90 km, 105 km, 120 km) have significant *r*-values, but there is not a pattern in the data. These distance classes have small sample sizes and may contain spurious correlations. Female hairy woodpeckers only have significantly positive *r*-values in the first distance class (15 km; Figure 6f; Table 5) while males have significantly positive *r*-values in the 15 and 45 km distance classes and at larger distance classes with small sample sizes (Figure 6e; Table 5).

Local spatial autocorrelation analysis

We performed 2D LSA on samples in eight burned areas for black-backed woodpeckers and three burned areas for hairy woodpeckers. In general, black-backed woodpeckers had a higher percentage of individuals within burned areas with significantly positive *lr*-values based on a one-tailed test (Table 6). Perhaps more telling is that the *lr*-values tended to be larger and more significant for black-backed woodpeckers than hairy woodpeckers (Table 6). When comparing the three burned areas that we performed the analyses for both species (BLM, WC, OR), black-backed woodpeckers had a higher percentage of clusters with stronger, more significant genetic correlations (Table 6). This pattern indicates that black-backed woodpeckers show a stronger signature of related groups within burned areas than hairy woodpeckers.

We did not detect a spatial pattern in the distribution of clusters within burned areas for either black-backed (Figure 7a) or hairy woodpeckers (Figure 7b). Based on visual assessment, a few burned areas show a slight pattern for black-backed woodpeckers (WC, OR, EC). The pattern is not consistent across sites or species and may or may not be relevant/spurious (Figure 7a). The lack of spatial pattern is not surprising given the spatial scale of the sites; all individuals within burned areas are less than 15 km apart.

The results from our temporal local spatial autocorrelation revealed a pattern of increased relatedness over time for black-backed woodpeckers (Figure 8a-c). Two burned areas (BM and OR) had genetic correlation values (*r*) that were significant in the first year the area was sampled (Figure 8a). Four burned areas (BM, OR, QB, WC) had significant genetic correlations in the second and third year the areas were sampled (Figure 8bc). Estimates of genetic correlation increased in four of the seven (57%) burned areas between year 1 and year 2. For hairy woodpeckers, we were only able to calculate a genetic correlation (*r*) for all years combined due to small sample sizes per year and did not detect any pattern of genetic correlation within burned areas (Figure 8d).

DISCUSSION

What is a breeding population?

In this study, we sampled in clustered manner, that is, we sampled multiple individuals at several different sites across a large spatial scale. Therefore, we chose to use both traditional population-level based analyses to define groups of individuals (AMOVA, SAMOVA, PCA, F_{ST}) and individual-based analyses (GENELAND). In both types of analyses, we used spatially implicit (AMOVA) and spatially explicit (SAMOVA, GENELAND) approaches. All of the approaches defined the same three populations, a large, genetically continuous population (Rocky Mountains across the boreal forest to Quebec) and two fragmented populations (Oregon and South Dakota). The spatially explicit approach employed in GENELAND displayed a very low level of uncertainty in estimating the number of populations. All ten runs estimated K= 3, with subsequent identification of population boundaries and assignment of individuals to the three populations incredibly consistent. Very few individuals were assigned to more than one population and all individuals assigned to the "correct" population with a probability > 0.99.

Behavioral barriers to movement

A recent review of patterns of genetic structure in seabirds found that areas between their breeding and nonbreeding distribution indicated potential barriers to dispersal (Friesen et al 2007), a similar pattern to what we found for female black-backed woodpeckers. However, black-backed woodpeckers' distribution closely follows the distribution of the boreal forest. Gaps created in the contiguous forest of the boreal, Rocky Mountains and Cascade regions are likely the ultimate cause of the limited gene flow across these geographic regions.

Evidence that large gaps in forested habitat are movement barriers for females can be seen in the population structure we detected and the difference in pairwise $F_{STmtDNA}$ values between sites that have large gaps in forest between them (fragmented: Oregon and South Dakota) as compared to sites that have forest between them (continuous: Idaho, Missoula, Glacier, Alberta and Quebec). Hierarchical population structure is a useful tool to detect barriers to gene flow when you have several subpopulations that may be connected by differing levels of gene flow (Allendorf and Luikart 2007). When sites within the Rocky Mountains are grouped with Quebec, we see a large amount of genetic variation among the groups and almost no genetic variation among the sites within group (Table 1). When we included Oregon with the Rocky Mountains and Quebec, the variation among sites increased 15 –fold, confirming a barrier likely exists between Oregon and the Rocky Mountains. Additional evidence can be seen in the high pairwise $F_{STmtDNA}$ values (0.36 – 0.75) between sites with large gaps in forest between them. These values are similar to what have been documented among subspecies or separate clades in other birds occupying similar ranges (Gibbs et al. 2000, Mila et al. 2007).

The inclusion of spatial data in GENELAND identified the general location of barriers to gene flow among the three populations (Figure 3). Sharp discontinuities in gene flow match the break in large forested areas between the Rocky Mountains and Oregon and the Rocky Mountains and South Dakota. However, the lack of samples in the boreal forest between Alberta and Quebec does not allow GENELAND to do a good job of assessing connectivity across the boreal forest.

Black-backed woodpeckers may not be a classic forest species due to their proclivity for burned forests in which most of the standing trees are dead, but it has been well documented that these birds prefer dense stands of dead trees (Saab et al. 2009). Organisms usually avoid dispersing through certain habitat types to avoid predators or a lack of resources during travel (Bélisle and Desrochers 2002). The risk of predation and the amount of resources available for foraging will be similar in burned and live forests than between any forest type and non-forest type (e.g., grassland, etc.). Therefore, it makes sense that black-backed woodpeckers would be averse to travelling long distances through non-forested habitat.

What is the average dispersal distance of black-backed vs. hairy woodpeckers?

We expect to see a significant positive genetic correlation among individuals when dispersal is limited (Peakall and Smouse 2006). Peakall et al. (2003) found that the scale at which positive genetic correlation persists in bush rats generally matched demographic data on dispersal distance. In birds, two studies have evaluated the usefulness of spatial autocorrelation techniques in assessing dispersal patterns by comparing demographic data to correlograms based on individually based genetic data (Double et al. 2005, Temple et al. 2006) and both found a high level of concurrence between data sets. Double et al. (2005) concluded that to fully exploit the power of spatial autocorrelation, you need highly variable markers, appropriate sampling and detailed ecological data such as age, sex and social status. Fortunately, we were able to obtain all of these variables. We sampled individuals both within and among fires at varying scales, used microsatellite markers, and only sampled breeding adults that were easily sexed based on morphological differences at the time of capture.

As predicted, black-backed woodpeckers showed a signal of positive genetic structure at twice the spatial scale (90 – 120 km) as hairy woodpeckers (45 km) indicating they tend to disperse twice as far. This is not surprising given black-backed woodpeckers high degree of specialization on burned areas. Hairy woodpeckers can disperse to many habitat types within range of their natal territory (Jackson et al. 2002) while black-backed woodpeckers rarely colonize unburned patches (Hutto 2008). Therefore, one would expect black-backed woodpeckers to disperse a larger distance from their natal territory in an attempt to locate optimal habitat patches.

Sex-biased dispersal pattern

Fine-scale analysis of genetic structure has confirmed the common pattern of male-biased dispersal in mammals (Coltman 2003, Nussey 2005) and female-biased dispersal in birds (Double et al. 2005, Temple et al. 2006). If one sex is responsible for the pattern of fine-scale structure present when both sexes are pooled, then we would expect to see a lack of structure in the dispersing sex when examined alone (Temple et al. 2006). Surprisingly, we found opposite patterns of sex-biased dispersal between these otherwise similar woodpeckers. Black-backed woodpeckers had a clear signal of male-biased dispersal and hairy woodpeckers had a weak, but present pattern of female-biased dispersal common in most bird species (Greenwood 1980). In black-backed woodpeckers; when the sexes are combined, there is a positive signal of genetic correlation up to 90 – 120 km. When females are examined alone, there is a positive genetic correlation up to 75 km, but males only have a positive genetic correlation in the smallest distance class, which is the scale within fires. This signal is likely due to delayed dispersal of juvenile males as opposed to differences in dispersal distance or rates between sexes. In contrast, female hairy woodpeckers only have a genetic correlation at the smallest spatial scale and males have a positive genetic correlation in the 15 and 45 km distance classes. Because we detected such a weak signal of sex-biased dispersal in hairy woodpeckers, more intensive research addressing this question needs to be conducted.

Kin groups/genetic clusters

Fine-scale genetic structure can be the result of family groups that exist when there is a high rate of natal philopatry or delayed juvenile dispersal. For example, many lekking species, such as red grouse, white-bearded manakins, and peacocks cluster in groups of related individuals (Petrie et al. 1999, Piertney et al. 1999, Shorey et al. 2000). Sex-biased dispersal can also lead to genetic clusters as a result of single-sex groups clustered if one sex tends to stay in or near the natal territory (Coltman 2003, Nussey 2005, Double et al. 2005, Lecomte et al. 2009). We wanted to test if family groups were present in burned areas as a result of delayed juvenile dispersal. If burned habitats are acting as a source due to higher quality of habitat, we predicted that juveniles would stay and exploit habitat that is high in food and nesting resources and delay the cost of dispersal. Additional benefits to delayed dispersal are the lack of aggression to kin in neighboring territories. We predicted we would see genetic clusters within burned areas as evidenced by the 2D LSA analysis and an increase of genetic relatedness (r) through time if this were indeed the case. Although this is a short time scale to assess changes in structure, Nussey et al. (2005) found spatial structure can change rapidly through time as a result of changes in population size and decreasing polygyny in red deer.

Indeed, all eight burned areas we assessed had a relatively large number of genetic clusters of black-backed woodpeckers (Figure 7) with strong signals of genetic correlation (Table 6). Hairy woodpeckers had few individuals with genetic clusters around them which potentially could be an artifact of incomplete sampling. We do not think this is the case because the burned area with the largest number of samples (OR) had a lower proportion of individuals with genetic clusters than any of the burned areas examined for black-backed woodpeckers.

Black-backed woodpeckers did show evidence of an increase in genetic relatedness over time in 57% of the burned areas we sampled, whereas hairy woodpeckers did show a signal of genetic correlation within burned areas. The accumulation of genetic relatedness over time for black-backed woodpeckers supports the hypothesis that juveniles are likely staying near their natal territory while the habitat patch is optimal. Although we were unable to test for a temporal increase in genetic correlation in hairy woodpeckers, the lack of a pattern in the pooled samples suggests there is a different dynamic occurring within burned areas for hairy woodpeckers as compared to black-backed woodpeckers. It appears juvenile dispersal may be delayed in black-backed woodpeckers which likely increases juvenile survival, further explaining how burned areas act as source habitat. Juvenile hairy woodpeckers may be hardwired to disperse from their natal territory prior to breeding regardless of the habitat type in which they are born.

How does the observed pattern of genetic variation inform the monitoring and management of populations?

Our data suggest that females do not cross large gaps in habitat and that large gaps in habitat act as a higher resistance landscape to long-distance dispersal for males. Therefore, small isolated populations, such as the one in South Dakota, may deserve higher priority for conservation. For example, land management actions that affect black-backed woodpecker habitat, such as salvage logging, would need to be considered in a spatial and temporal context because fewer habitat patches are available to birds through time. If the population in South Dakota declines due to habitat degradation, recolonization of the areas by females is unlikely. Additionally, it is important to determine if the Oregon population is connected to California or Washington populations when planning management actions that affect populations. Within the boreal forest, it is evident that there have been high levels of gene flow for a long time. Management actions should strive to maintain forested connectivity between burned patches to maintain these levels of gene flow.

Early post-fire habitat has long been thought to provide source habitat for woodpecker species because abundance and nest success is higher in burned areas vs. unburned areas for species that occupy both habitat types (Hutto 1995, Nappi and Drapeau 2009). Burned forest may provide source habitat for both woodpecker species we studied by providing an excess of individuals due to high reproduction. We found black-backed woodpeckers likely disperse less than 100 km, providing the first details on the spatial scale that these burned areas provide migrants. Our results confirm banding studies that show hairy woodpeckers only disperse ~40 km (Jackson et al. 2002). Black-backed woodpeckers likely move longer distances because they are more reliant on burned forest for habitat, whereas hairy woodpeckers can successfully reproduce in many habitat types. It may be that unburned forests are a more detrimental sink to black-backed populations than hairy woodpecker populations, forcing black-backed woodpeckers to search farther for burned forest.

This research has provided insight into the dynamics of how burned forest may function as source habitat through increased juvenile survival. The temporal increase in genetic clusters in 57% (four of seven) burned areas sampled supports our hypothesis that juvenile black-backed woodpeckers are delaying dispersal and thereby enjoying a higher rate of survival. Although burned patches may provide excellent short term resources for hairy woodpeckers, the same dynamics are not occurring within burned forest for these two species. To confirm whether burned areas act as sources for both species, the best approach is to detect asymmetrical migration from sources to sinks. The use of genetic techniques to detect such a pattern shows great promise (Manier and Arnolf 2005, Hänfling and Weetman 2006, Peery et al. 2008) if sampling is possible in both source and sink habitats. Unfortunately, black-backed woodpeckers are extremely rare in unburned habitat (Hutto 2008) and we were unable to obtain the samples necessary to take advantage of these approaches.

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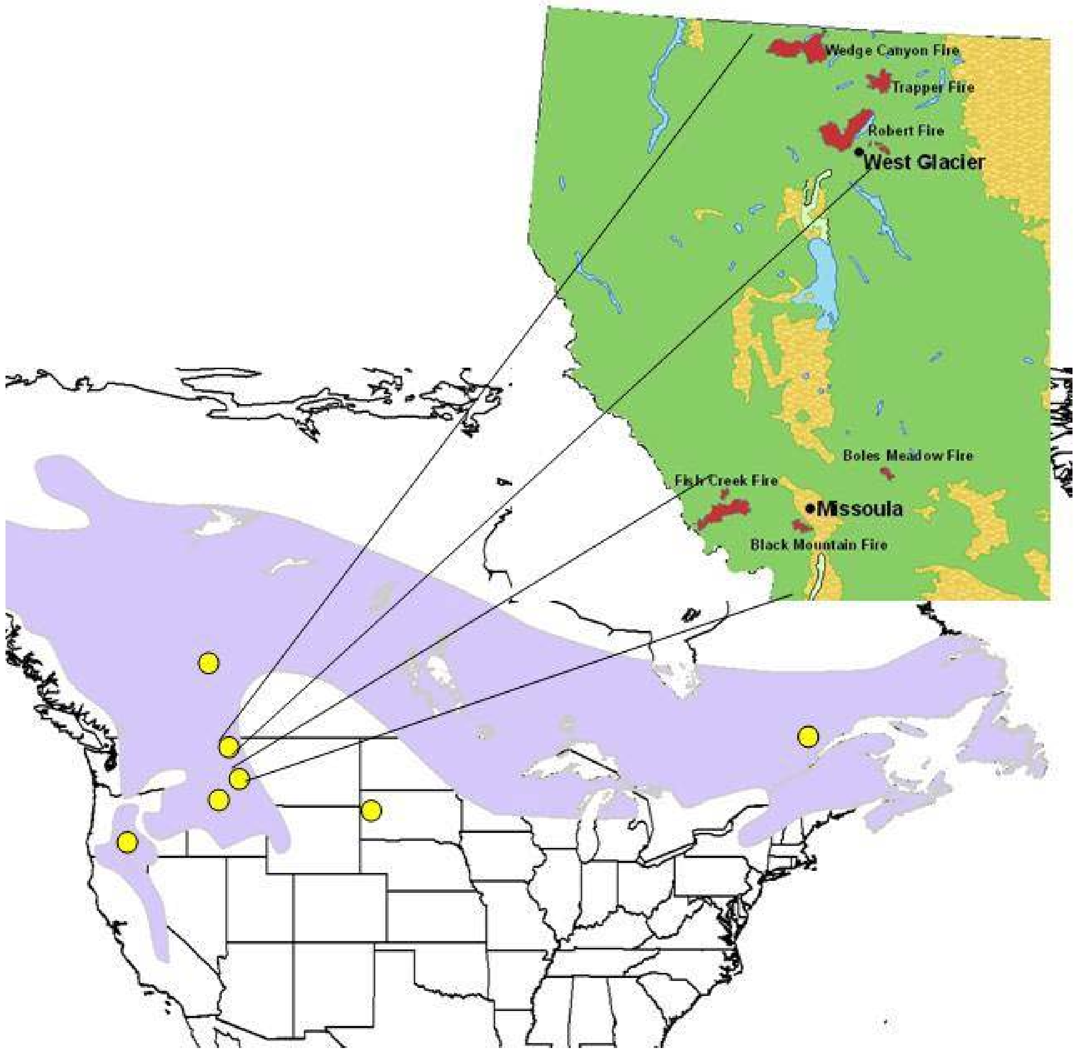
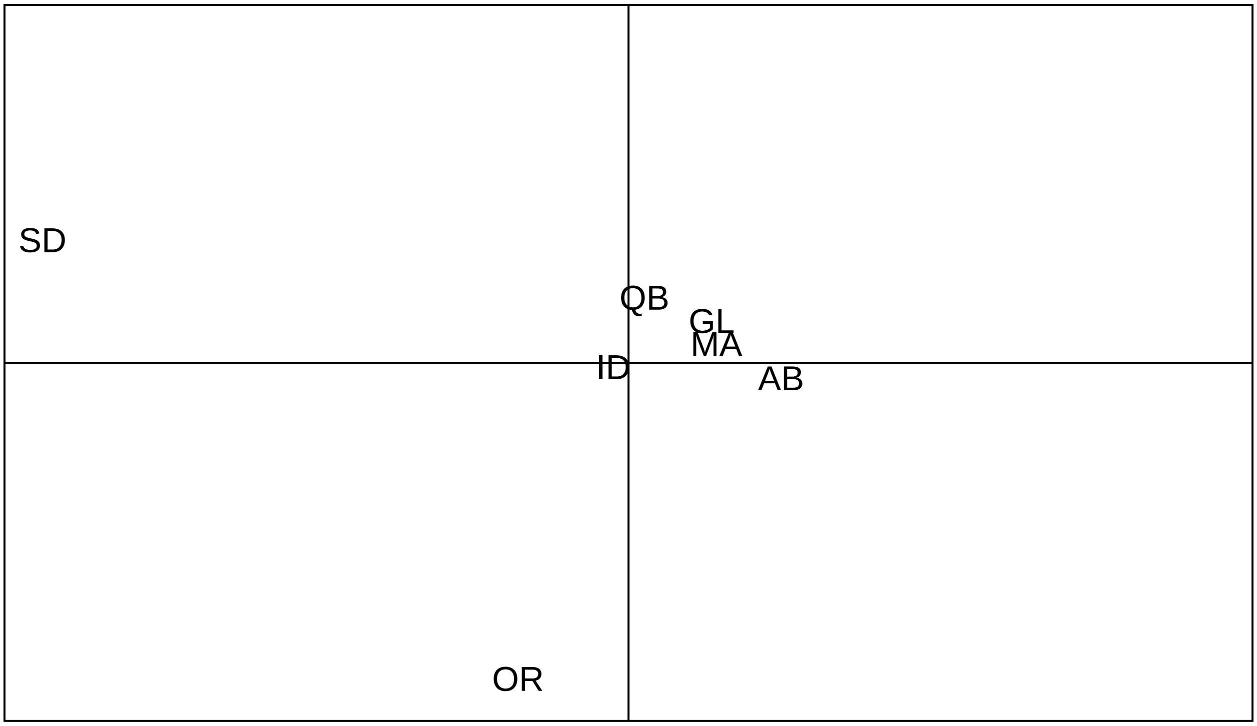


Figure 1. (a) A map of the United States and Canada showing the hierarchical sampling design including (a) the location of the seven broad-scale study sites: GL: Glacier National Park; MSLA: Missoula, MT; OR: Silver Lake, Oregon; EC: Eastern Canada; SD: Black Hills, South Dakota; ID: central Idaho; AB: Jasper National Park, Alberta and (b) the two study sites within western Montana that each have three areas that burned in 2003: Missoula – BLM: Black Mountain fire; BM: Boles Meadow fire; FC: Fish Creek fire and Glacier National Park – WC: Wedge Canyon fire; RB: Robert fire; TR: Trapper fire

a)



b)

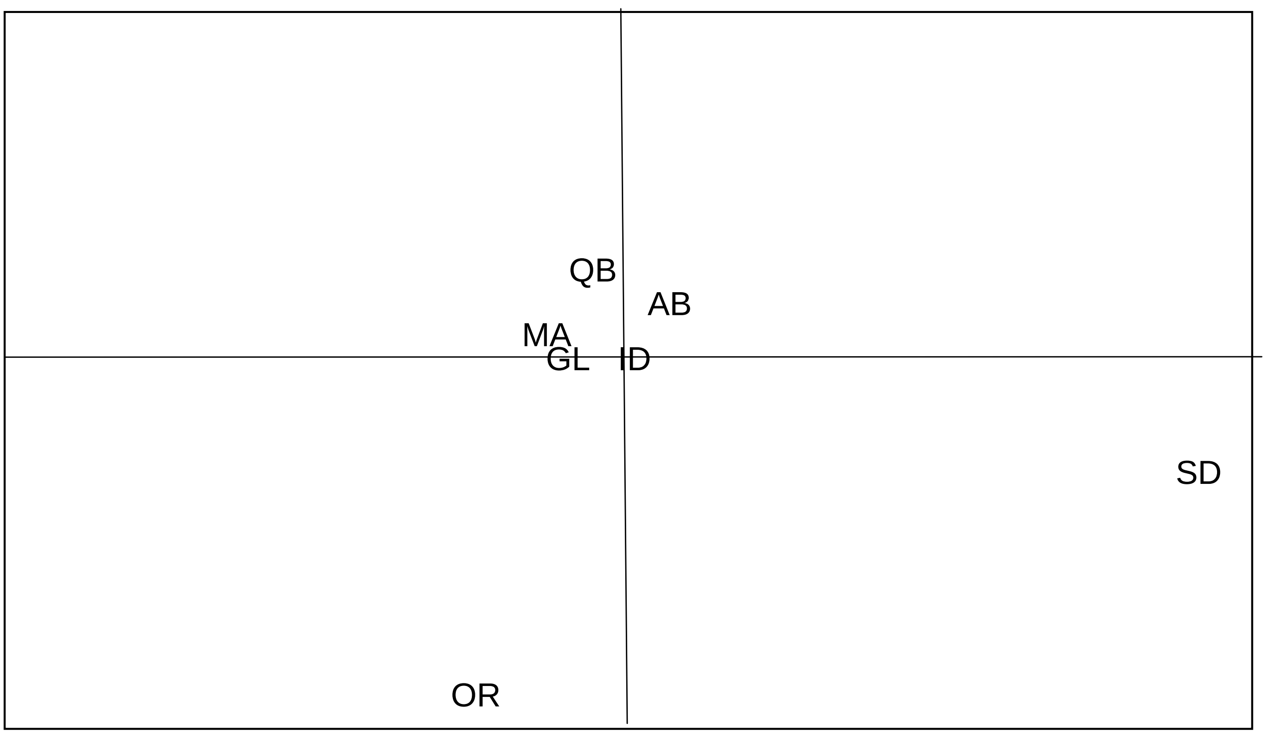


Figure 2. Principal Components Analysis visualizing clustering of sampling locations based on a) mtDNA; PC 1 = 59%, PC 2 = 39%; b) microsatellite data, PC 1 = 38%, PC 2 = 29%; SD = South Dakota, OR = Oregon, ID = Idaho, MA = Missoula, GL = Glacier, AB = Alberta, QB = Quebec.

a)

b)

c)

d)

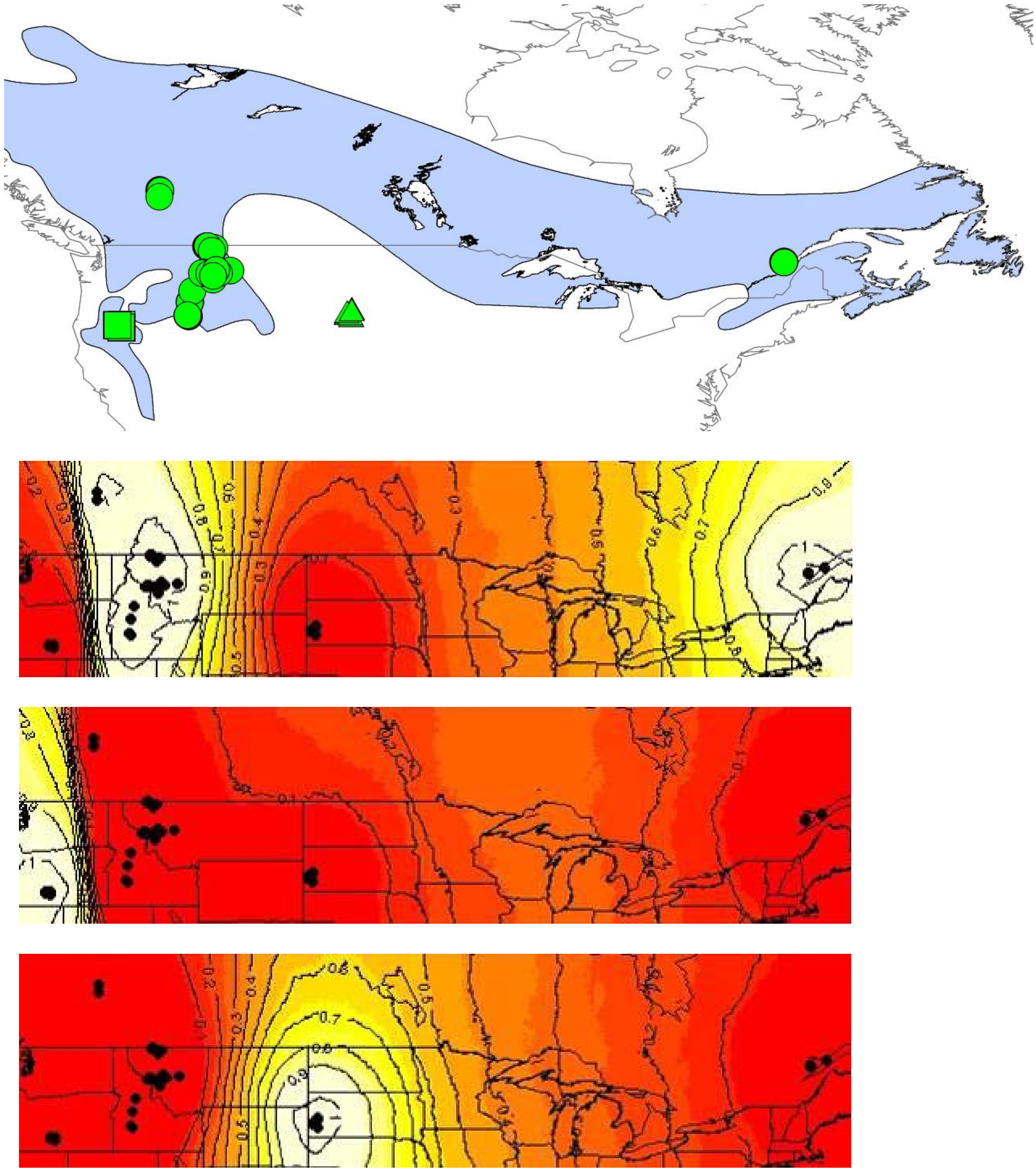


Figure 3. Maps showing the three clusters identified in the spatially explicit analysis conducted in GENELAND. Figure (a) identifies which cluster each sample was grouped with in assignment tests conducted in GENELAND (circles = continuous population extending from the Rocky Mountains to Quebec; squares = Oregon; triangles = South Dakota)The three clusters are b) continuous population extending from the Rocky Mountains to Quebec, c) western population, d) South Dakota population. The contours represent probability of assignment to the clusters and display where barriers to gene flow exist. The appearance of a partial barrier to gene flow within (a) is likely an artifact

of the lack of samples between Alberta and Quebec given samples at each end of this cluster assign with a high probability to the same population.

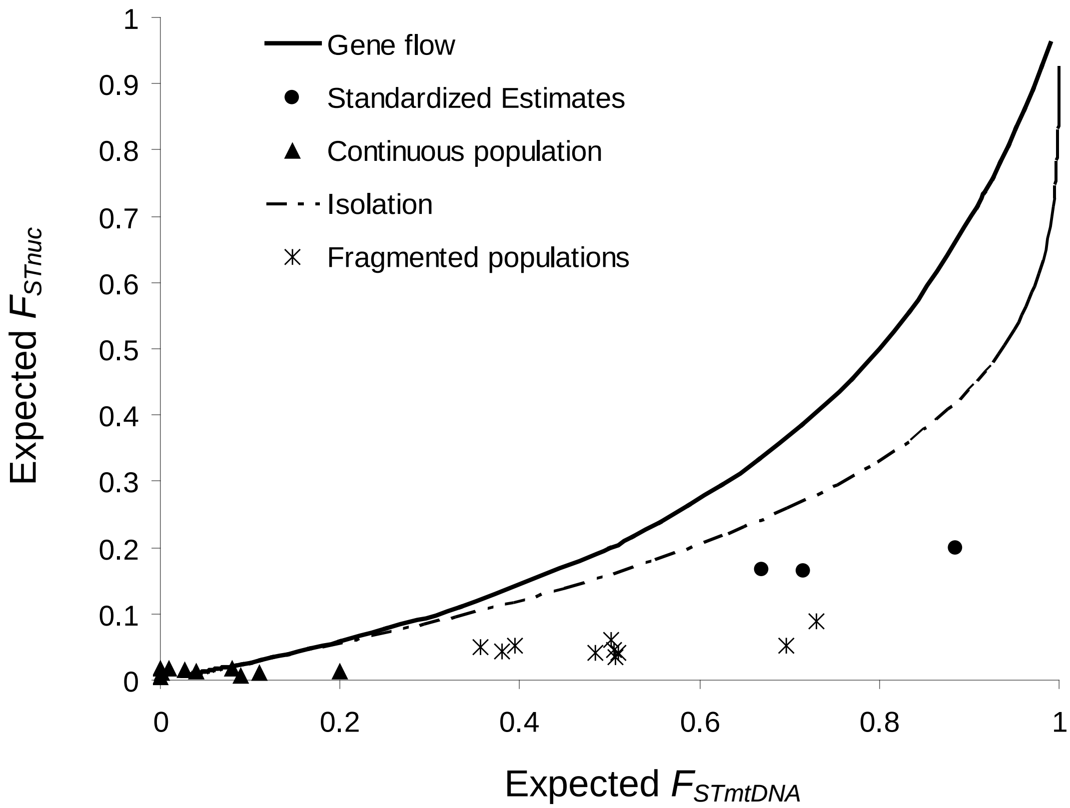


Figure 4. The expected relationship between F_{STnuc} and $F_{STmtDNA}$ at mutation-drift equilibrium under Wright's island model of migration (solid black line) and under a model of isolation (dashed line). Observed pairwise values of F_{STmsat} and $F_{STmtDNA}$ for black-backed woodpeckers are plotted; black triangles are sites within the continuous distribution, asterisks are pairwise values where at least one of the pair are in the fragmented sites and solid black circles are standardized estimates between the three populations inferred from both hierarchical population analyses and individual-level clustering in GENELAND.

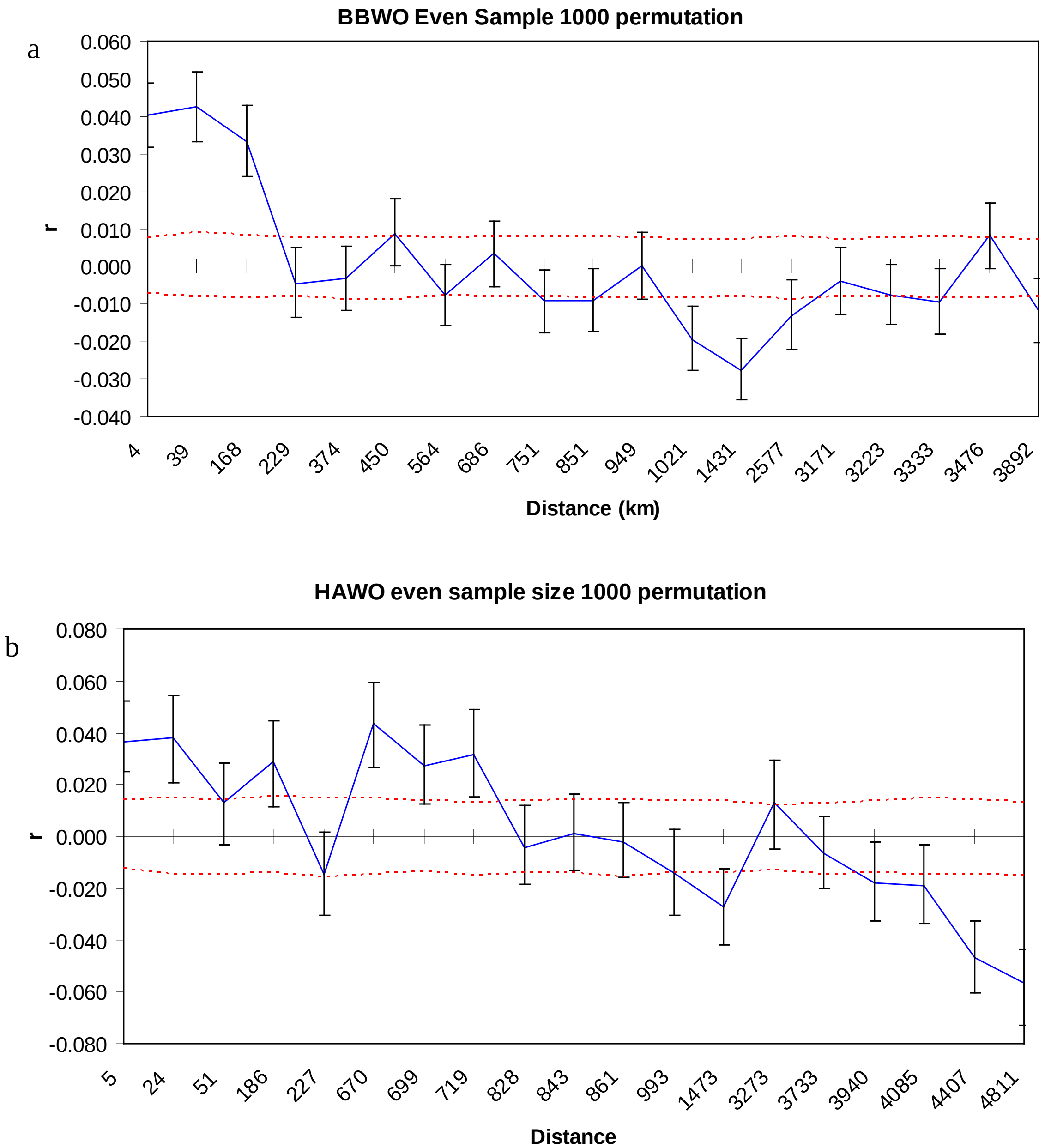
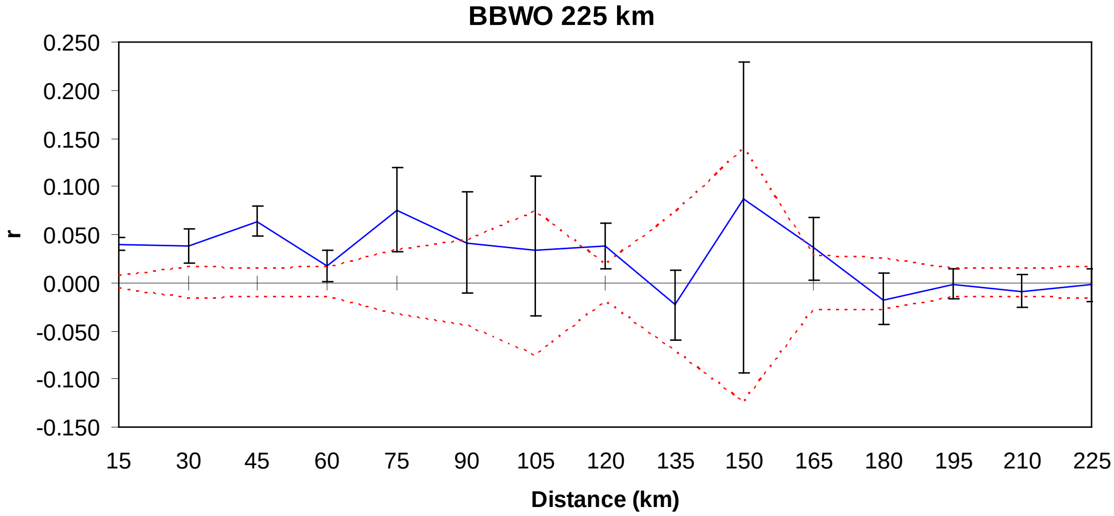
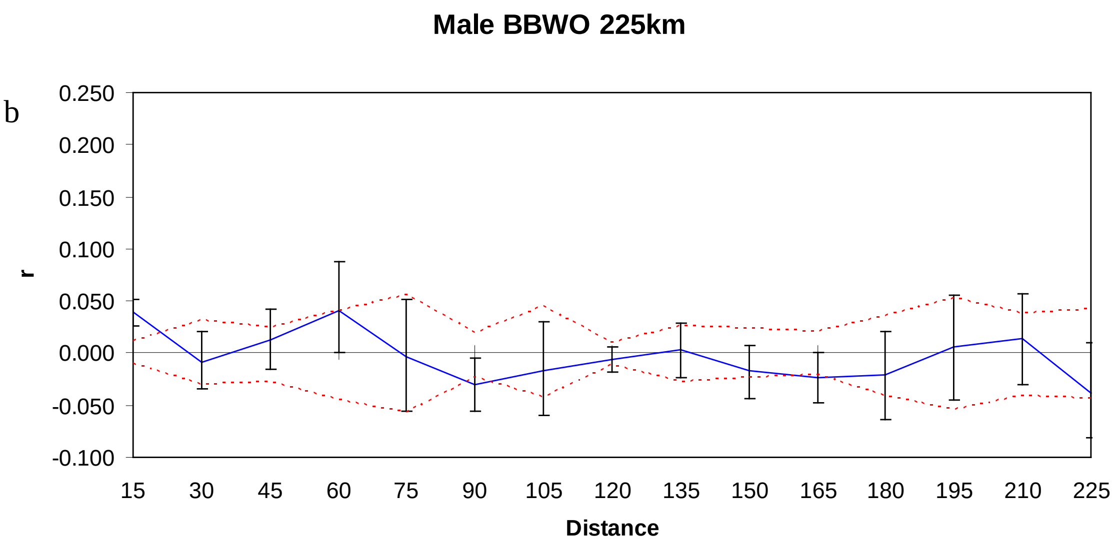


Figure 5. Correlogram plots based on global spatial autocorrelation analyses conducted at the broadest spatial scale using the even sample size per distance class option. The y-axis is the genetic correlation coefficient (*r*) and the x-axis is the distance class (km). 95% confidence intervals were calculated using bootstrapping (error bars) and permutation tests (dashed lines). (a) black-backed woodpeckers (b) hairy woodpeckers.

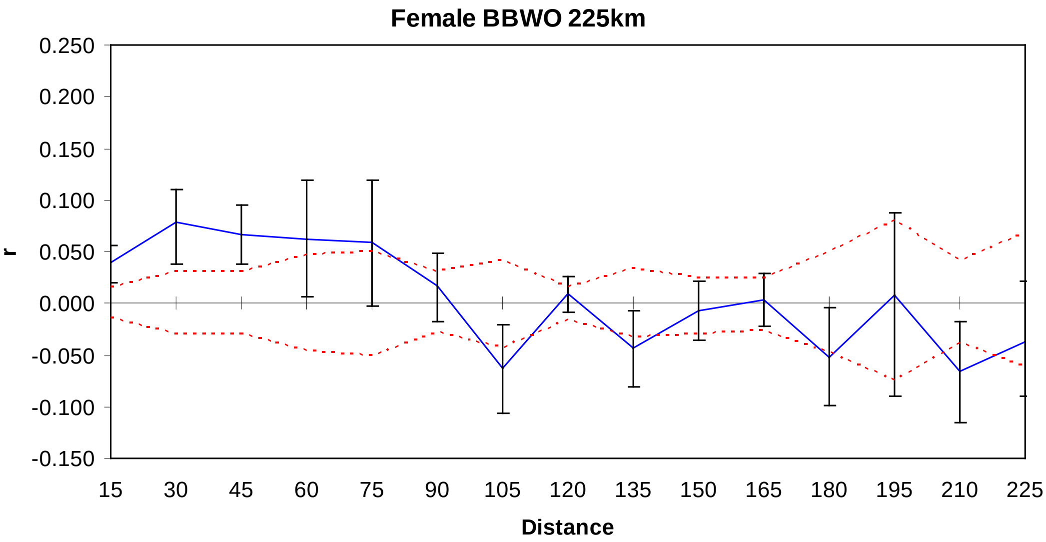
a


BBWO 225 km
r
0.250
0.200
0.150
0.100
0.050
0.000
-0.050
-0.100
-0.150
15 30 45 60 75 90 105 120 135 150 165 180 195 210 225
Distance (km)

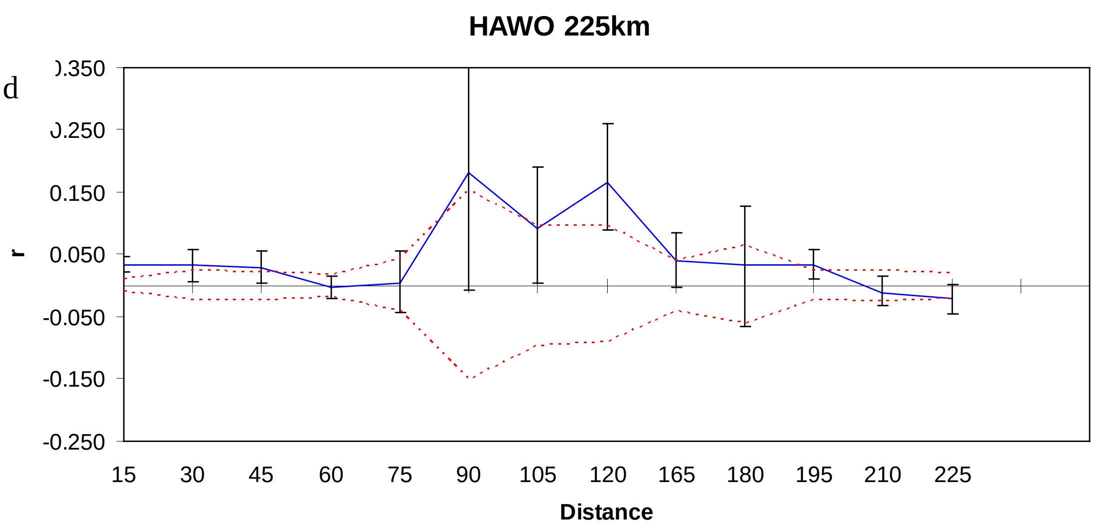
b

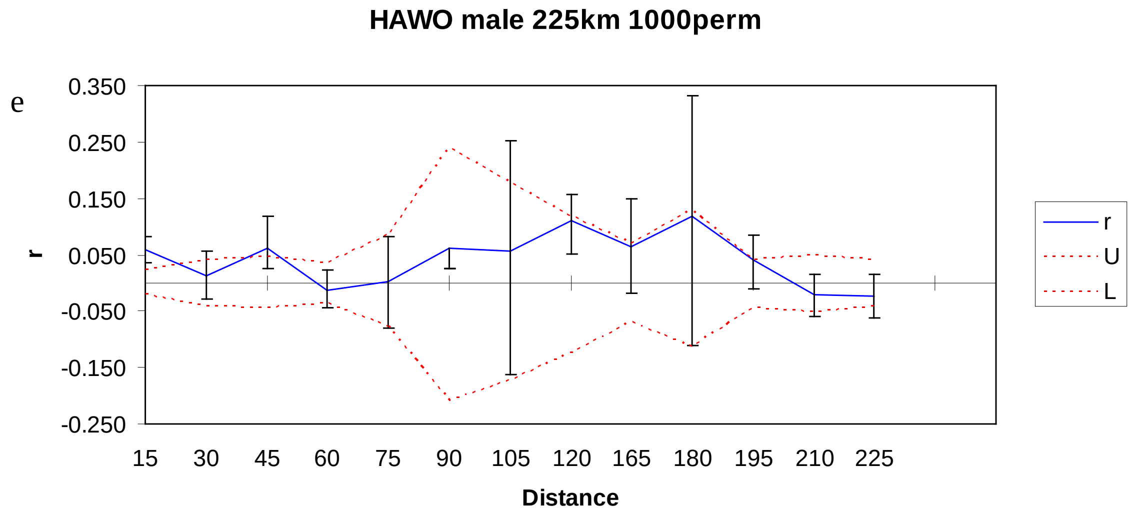

Male BBWO 225km
r
0.250
0.200
0.150
0.100
0.050
0.000
-0.050
-0.100
15 30 45 60 75 90 105 120 135 150 165 180 195 210 225
Distance

c


Female BBWO 225km
0.250
0.200
0.150
0.100
0.050
0.000
-0.050
-0.100
-0.150
r
15 30 45 60 75 90 105 120 135 150 165 180 195 210 225
Distance

d


HAWO 225km
0.350
0.250
0.150
0.050
-0.050
-0.150
-0.250
r
15 30 45 60 75 90 105 120 165 180 195 210 225
Distance



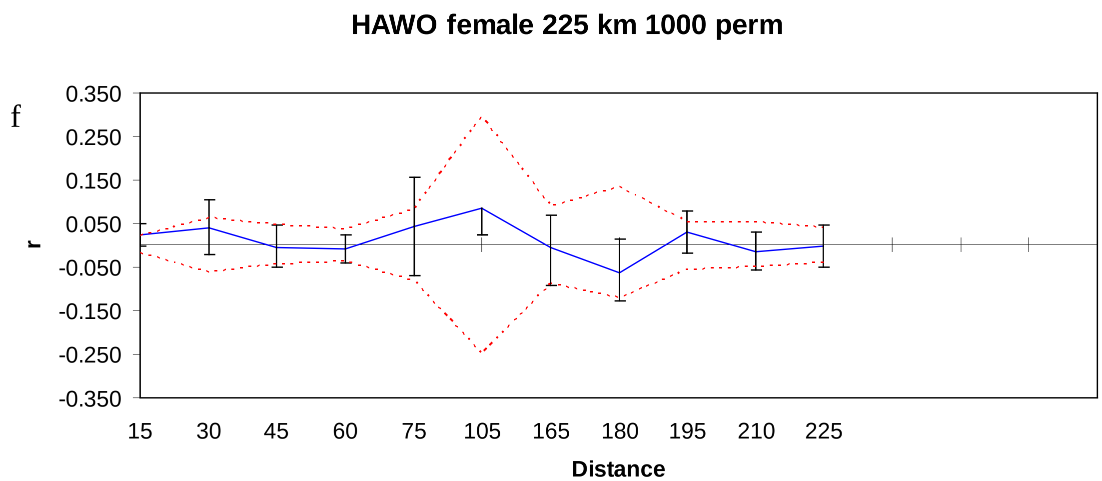
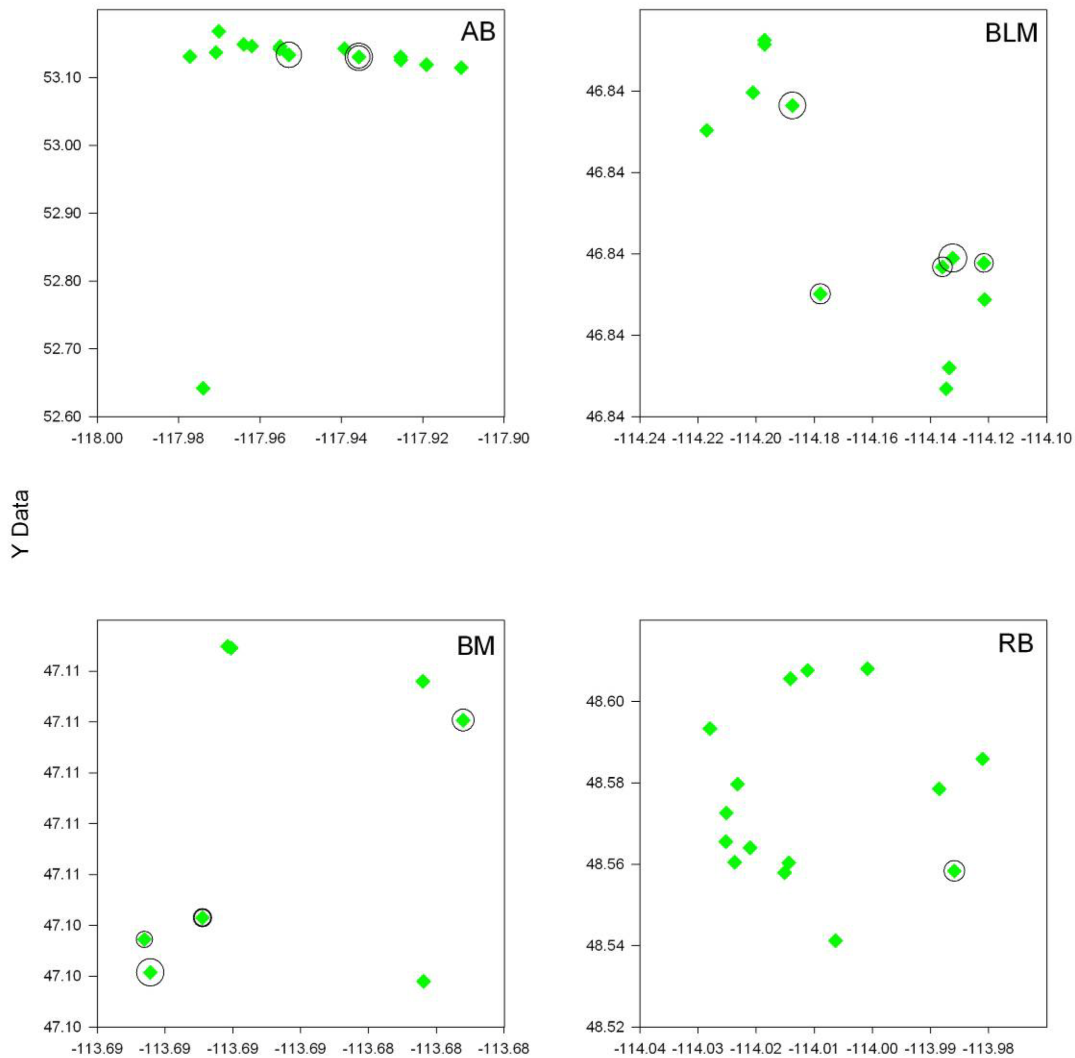
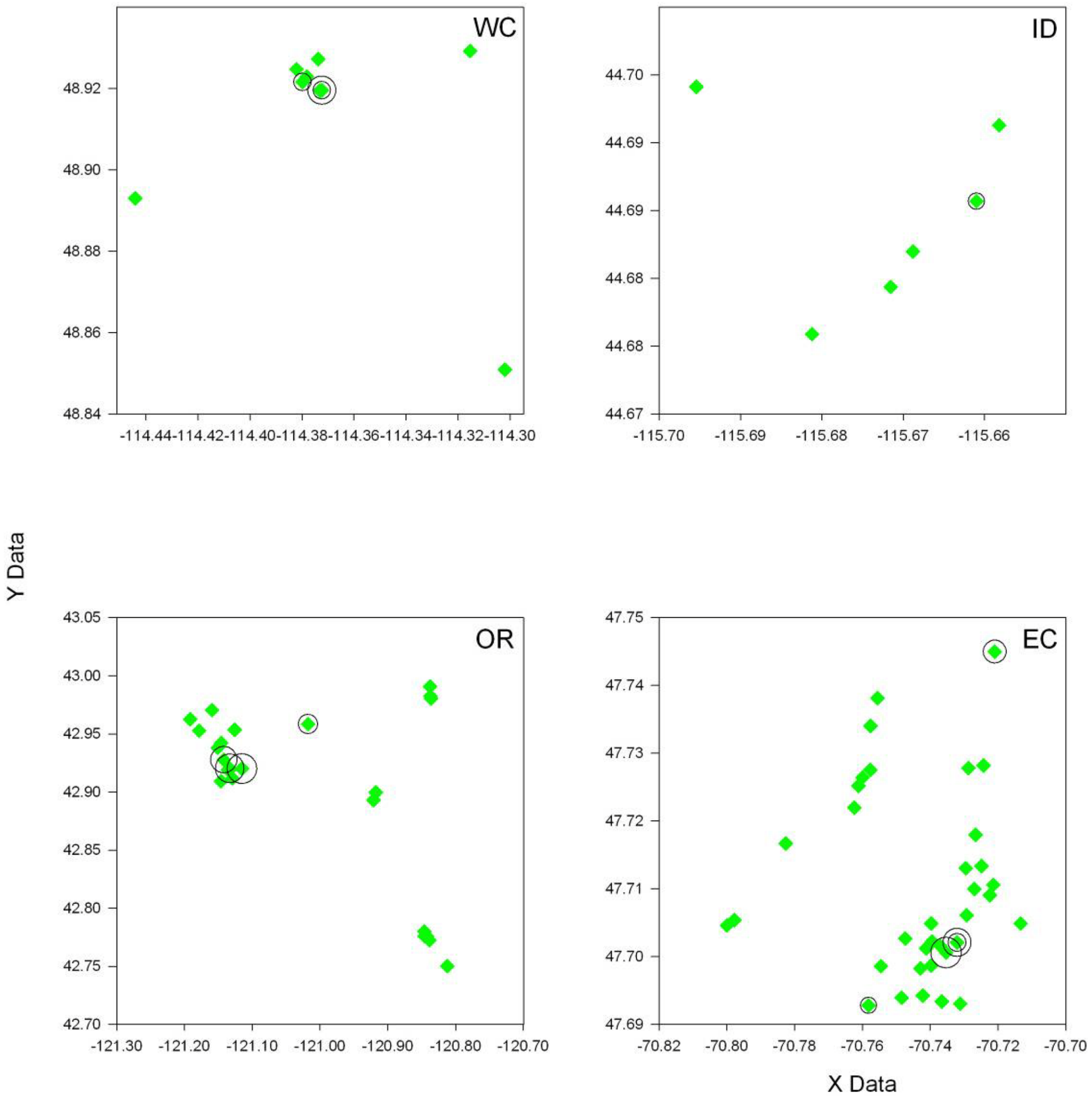


Figure 6. Correlogram plots based on global spatial autocorrelation analyses conducted with 15km distance classes up to 225 km The y-axis is the genetic correlation coefficient (*r*) and the x-axis is the distance class (km). 95% confidence intervals were calculated using bootstrapping (error bars) and permutation tests (dashed lines). (a) black-backed woodpeckers, (b) male black-backed woodpeckers, (c) female black-backed woodpeckers, (d) hairy woodpeckers, (e) male hairy woodpeckers, and (f) female hairy woodpeckers.

a



AB
BLM
BM
RB
Y Data
53.10
53.00
52.90
52.80
52.70
52.60
-118.00 -117.98 -117.96 -117.94 -117.92 -117.90
46.84
-114.24 -114.22 -114.20 -114.18 -114.16 -114.14 -114.12 -114.10
47.11
47.10
-113.69 -113.69 -113.69 -113.69 -113.68 -113.68 -113.68
48.60
48.58
48.56
48.54
48.52
-114.04 -114.03 -114.02 -114.01 -114.00 -113.99 -113.98


WC
ID
OR
EC
Y Data
X Data
48.84
48.86
48.88
48.90
48.92
-114.44-114.42-114.40-114.38-114.36-114.34-114.32-114.30
44.67
44.68
44.68
44.69
44.69
44.70
-115.70
-115.69
-115.68
-115.67
-115.66
42.70
42.75
42.80
42.85
42.90
42.95
43.00
43.05
-121.30
-121.20
-121.10
-121.00
-120.90
-120.80
-120.70
47.69
47.70
47.71
47.72
47.73
47.74
47.75
-70.82
-70.80
-70.78
-70.76
-70.74
-70.72
-70.70

b

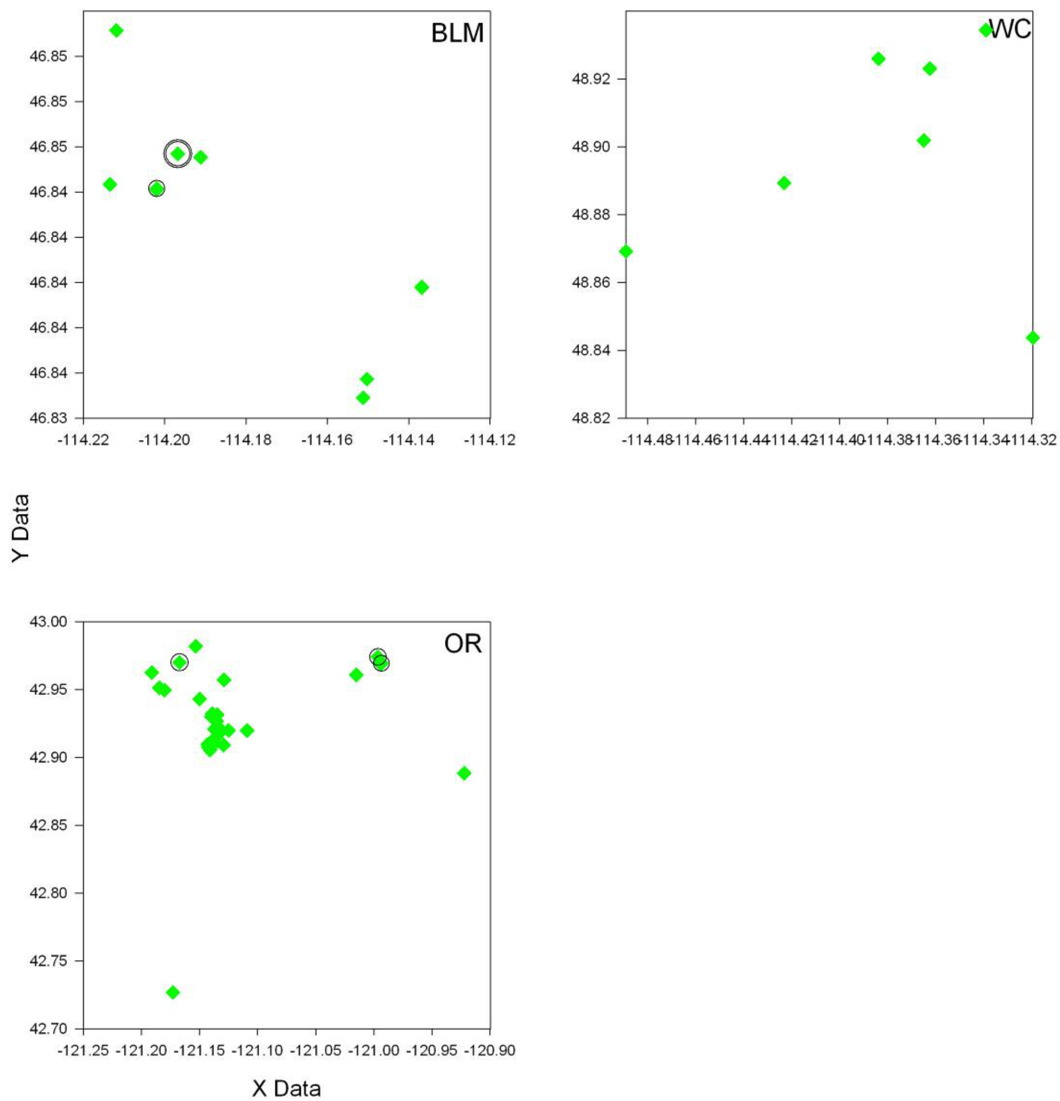
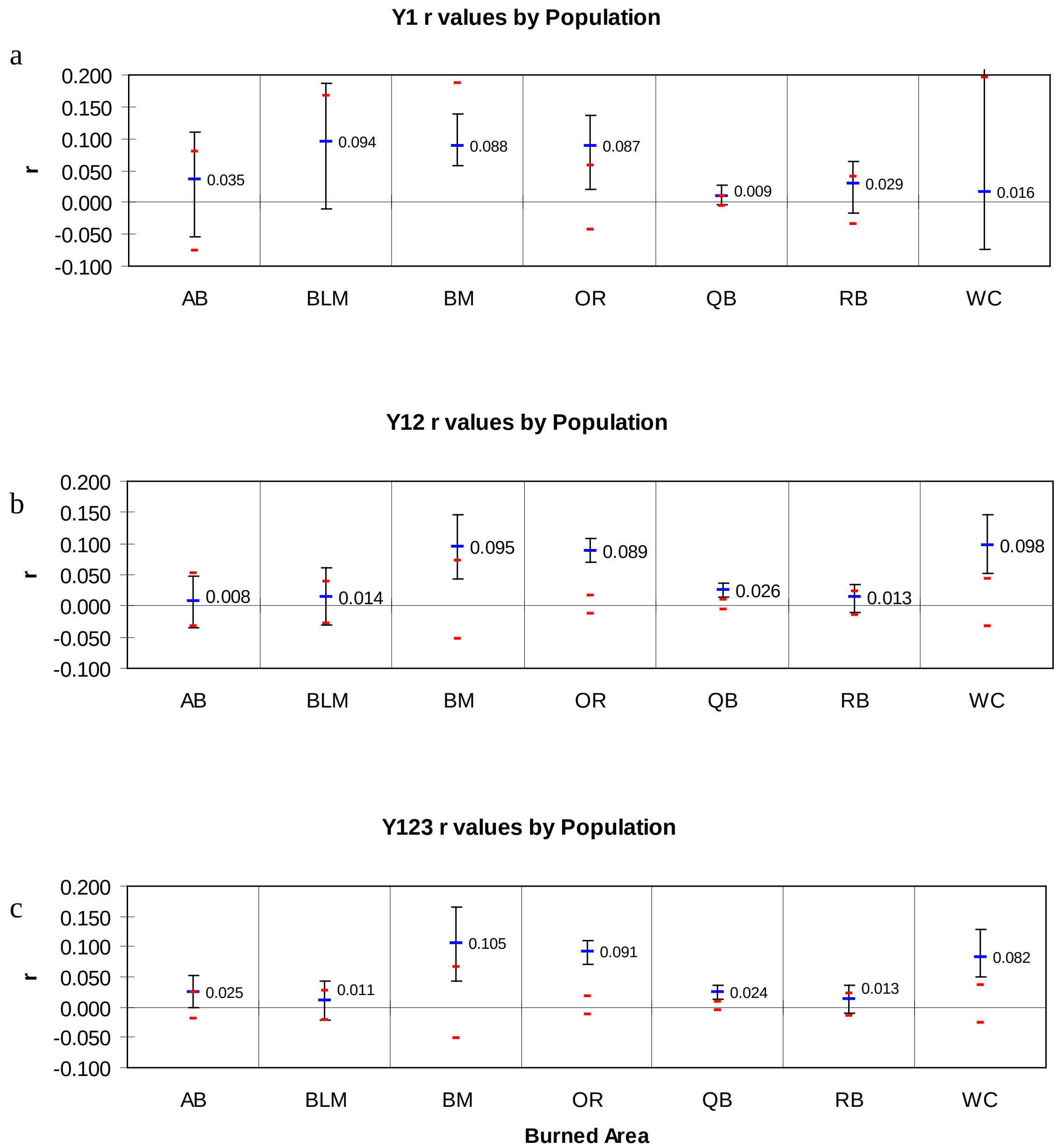


Figure 7. Bubble plots of the two-dimensional local spatial autocorrelation (2D LSA) based on the five nearest neighbors for (a) black-backed woodpeckers and (b) hairy woodpeckers. Each bubble plot displays significant genetic clusters, based on one-tailed permutation tests, detected around individual woodpeckers within each burned area with more than 10 individual woodpecker samples. The size of the circle represents the strength of the genetic correlation detected using 2D LSA analysis in Genalex. Axis are latitude and longitude locations of individuals. AB: Alberta; BLM: Black Mountain fire in Missoula, MT; BM: Boles Meadow fire in Missoula, MT; RB: Robert fire in Glacier National Park; MT, WC: Wedge Canyon fire in Glacier National Park; MT, ID: central Idaho; OR: Oregon; EC: Eastern Canada


Y1 r values by Population
a
r
0.200
0.150
0.100
0.050
0.000
-0.050
-0.100
0.035
0.094
0.088
0.087
0.009
0.029
0.016
AB
BLM
BM
OR
QB
RB
WC
Y12 r values by Population
b
r
0.200
0.150
0.100
0.050
0.000
-0.050
-0.100
0.008
0.014
0.095
0.089
0.026
0.013
0.098
AB
BLM
BM
OR
QB
RB
WC
Y123 r values by Population
c
r
0.200
0.150
0.100
0.050
0.000
-0.050
-0.100
0.025
0.011
0.105
0.091
0.024
0.013
0.082
AB
BLM
BM
OR
QB
RB
WC
Burned Area

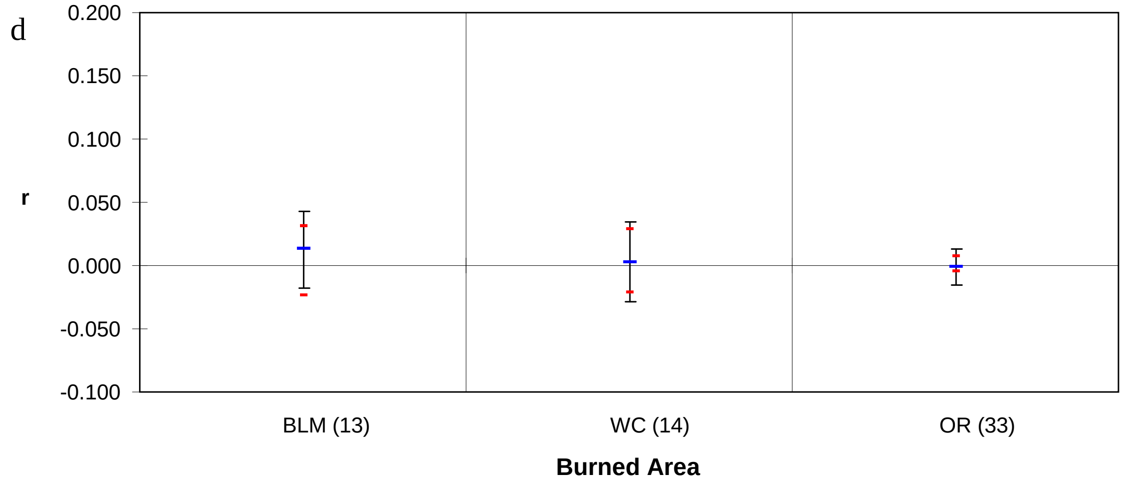


Figure 8. Temporal estimates of genetic correlation coefficients (*r*) within each burned area with at least 10 individuals sampled (see Figure 4 for location descriptions). The 95 % confidence intervals are based on both bootstrapping (error bars surrounding estimates) and permutations (error bars surrounding null expectation of 0); (a) year one of sampling black-backed woodpeckers (b) year one and two pooled for black-backed woodpeckers, (c) year one, two and three pooled for black-backed woodpeckers. (d) year one, two and three pooled together for hairy woodpeckers; samples sizes were too small to do a temporal analysis.

Table 1. Analysis of molecular variance (AMOVA) results of five different groupings of black-backed woodpecker sampling sites for mtDNA and microsatellite loci. Significance values are based on 1000 permutations using ARLEQUIN 3.11. Results from spatial analysis of molecular variance (SAMOVA) are nearly identical and therefore, are not shown.

Group	No. of groups	Variance component	mtDNA % of variance	Microsatellites % of variance
(Rocky Mountains[1] + Quebec+ Oregon) (South Dakota)	2	Among groups	35.26	3.18
		Among sites	15.24**	2.22**
		Within sites	49.5**	94.61**
(Rocky Mountains[1] + Quebec) (Oregon) (South Dakota)	3	Among groups	49.99*	3.54*
		Among sites	1.07*	1.38**
		Within sites	48.95**	95.08**
(Rocky Mountains[1]) (Quebec) (Oregon) (South Dakota)	4	Among groups	37.51	2.33
		Among sites	1.4	1.27**
		Within sites	61.08**	96.4**
(W. Montana + N.W. Montana + Idaho + Quebec) (Alberta) (Oregon) (South Dakota)	4	Among groups	45.01*	2.71*
		Among sites	0.12	1.41**
		Within sites	54.87**	95.88**
(Missoula + Glacier) (Idaho) (Alberta) (Quebec) (Oregon) (South Dakota)	6	Among groups	34.13	1.9
		Among sites	-1.03	1.18**
		Within sites	66.90**	96.93**

[1]Rocky Mountains = Idaho, W, Montana, N.W. Montana, Alberta; * *P* , 0.05; ** *P* < 0.0001

Table 2. Genetic diversity for all sampling locations, including the number of individuals sampled (n), number of haplotypes observed at each location, haplotype diversity (h), nucleotide diversity (π), haplotype richness (HR); F_{IS}, fixation index; H_E, expected heterozygosity; AR, allelic richness; standard errors are in parentheses.

	n	No. of haplotypes	h	π	HR	F_{IS}	H_E	AR
Idaho	42	6	0.616 (0.012)	0.004	4.57	-0.01	0.58	5.46 (1.35)
Missoula	49	6	0.450 (0.012)	0.002	4	0.12	0.58	5.52 (1.18)
Glacier	48	7	0.457 (0.012)	0.002	4.12	0.01	0.58	5.69 (1.15)
Alberta	21	2	0.324 (0.024)	0.002	1.98	0.02	0.63	6.36 (1.30)
Quebec	56	12	0.589 (0.010)	0.002	5.58	0.05	0.6	5.76 (1.38)
Oregon	32	3	0.462 (0.013)	0.003	2.47	0.08	0.58	5.13 (0.90)
S. Dakota	27	2	0.074 (0.013)	0.001	1.55	0.01	0.46	3.57 (0.52)
All locations	275	18	0.613 (0.029)	0.003		0.05	0.6	6.03 (1.33)

Table 3. Pairwise F_{ST} values for mtDNA (below diagonal) and microsatellite (above diagonal). Significant values are indicated in bold and with asterisks

	Idaho	Missoula	Glacier	Alberta	Quebec	Oregon	S. Dakota
Idaho		**0.007*****	**0.015****	**0.022*****	**0.019*****	**0.048*****	**0.057*****
Missoula	0.000		**0.012*****	**0.014*****	**0.014*****	**0.035*****	**0.044*****
Glacier	0.001	0.000		**0.012***	**0.017*****	**0.042*****	**0.049*****
Alberta	0.040	**0.092****	**0.08*****		0.006	**0.050*****	**0.050*****
Quebec	0.028	0.000	0.000	**0.11****		**0.049*****	**0.056*****
Oregon	**0.38*****	**0.51*****	**0.51*****	**0.36*****	**0.54*****		**0.094*****
S. Dakota	**0.43*****	**0.51*****	**0.54*****	**0.73*****	**0.53*****	**0.75*****	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 4. Observed and standardized pairwise F_{ST} estimates between inferred populations ; mtDNA (below diagonal) and microsatellite (above diagonal).

Observed F_{ST}				Standardardized F_{ST}			
	Continuous	Oregon	S. Dakota		Continuous	Oregon	S. Dakota
Continuous		0.039	0.043	Continuous		0.165	0.167
Oregon	0.490		0.095	Oregon	0.716		0.200
S. Dakota	0.452	0.754		S. Dakota	0.669	0.885	

Table 5. Results from a one-tailed test for positive genetic autocorrelation (*r*) which is expected when there is limited dispersal for black-backed (BBWO) and hairy woodpeckers (HAWO) including both sexes, then males and females separately. The number of pairwise comparisons (n) per distance class (km) and the probability the estimated *r* is greater than expected based on 1000 permuations (P); significant values are indicated in bold

	Distance class (km)	**15**	**30**	**45**	**60**	**75**	**90**	**105**	**120**	**135**	**150**	**165**	**180**	**195**	**210**	**225**
BBWO BOTH	**n**	2976	526	599	617	121	69	24	321	31	8	157	190	597	583	429
	Prob r > perm. r	0.001	0.001	0.001	0.013	0.001	0.038	0.180	0.001	0.739	0.105	0.004	0.908	0.599	0.899	0.608
BBWO MALE	**n**	960	152	177	71	39	225	67	846	168	195	260	89	46	79	69
	Prob r > perm. r	0.001	0.726	0.173	0.025	0.550	0.996	0.769	0.852	0.390	0.910	0.985	0.870	0.405	0.242	0.956
BBWO FEMALE	**n**	492	134	147	57	49	125	65	417	105	161	166	52	20	70	30
	Prob r > perm. r	0.001	0.001	0.001	0.006	0.014	0.141	0.997	0.122	0.995	0.709	0.387	0.983	0.399	1.000	0.871
HAWO BOTH	**n**	726	156	161	229	52	4	10	11			53	22	141	128	184
	Prob r > perm. r	0.001	0.005	0.005	0.586	0.408	0.009	0.033	0.001			0.033	0.158	0.005	0.816	0.971
HAWO MALE	**n**	180	55	48	68	15	2	3	7			19	7	47	37	50
	Prob r > perm. r	0.001	0.249	0.004	0.745	0.474	0.268	0.269	0.034			0.038	0.033	0.029	0.786	0.876
HAWO FEMALE	**n**	161	21	34	47	11		1				9	5	25	27	42
	Prob r > perm. r	0.015	0.084	0.562	0.668	0.149		0.281				0.549	0.839	0.134	0.689	0.548

Table 6. The number of individuals included (N) in 2D LSA for each location, the percent of individuals that had significant genetic clusters surrounding them, including the range of significance values and local genetic autocorrelation values (*lr*). AB: Alberta, BLM: Black Mountain fire in Missoula, MT, BM: Boles Meadow fire in Missoula, MT, RB: Robert fire in Glacier National Park, MT, WC: Wedge Canyon fire in Glacier National Park, MT, ID: central Idaho, OR: Oregon.

	Location	N	N significant	% significant	P-value range	*lr* range
BBWO	AB	21	3	14	0.005 - 0.011	0.20 - 0.24
	BLM	21	5	24	0.003 - 0.026	0.17 - 0.25
	BM	11	5	45	0.003 - 0.045	0.15 - 0.24
	RB	24	1	04	0.018	0.18
	WC	16	3	19	0.004 - 0.032	0.16 - 0.25
	ID	10	1	10	0.041	0.14
	OR	29	4	14	0.002 - 0.02	0.17 - 0.26
	EC	49	5	10	0.003 - 0.041	0.14 - 0.27
HAWO	BLM	13	3	23	0.01 - 0.03	0.14 - 0.24
	WC	14	0	00	NA	NA
	OR	33	3	09	0.01 - 0.04	0.14 - 0.15